

RANDOMNESS AND DIVERSIFICATION IN THE PHANEROZOIC: A SIMULATION

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ABSTRACT. The essential features of the pattern of marine animal diversification in the Phanerozoic are reproduced by a stochastic, quasi-random simulation. The model assumes only (i) random variation in the origination and extinction of lineages and (ii) occurrence of two extraordinary events: 'Late Cambro-Ordovician radiation' and 'Late Permo-Triassic extinction'. It can mimic the shape of the curve of global diversity as well as the pattern of so-called evolutionary faunas.

THE pattern and process of change in global taxonomic diversity during the Phanerozoic have long been among the focal points of palaeobiological research. Sepkoski (1978, 1979, 1984) and Sepkoski and Sheehan (1983) developed a multiphase logistic model to account for the empirical pattern of marine animal diversification (Sepkoski *et al.* 1981; Sepkoski 1982). The model assumes diversity dependence of the processes of origination and extinction of taxa, which should bring the biosphere to a dynamic equilibrium. It envisages three large groups of marine animal classes, or evolutionary faunas, as identified by factor analysis of their diversity histories (Sepkoski 1981). Each evolutionary fauna has its own characteristic parameters of diversity dependence, but each fauna also responds to the total diversity and thus interacts with the other two faunas. When this purely biological model is complemented with mass extinctions as extrinsic perturbations, it fits the empirical pattern quite well.

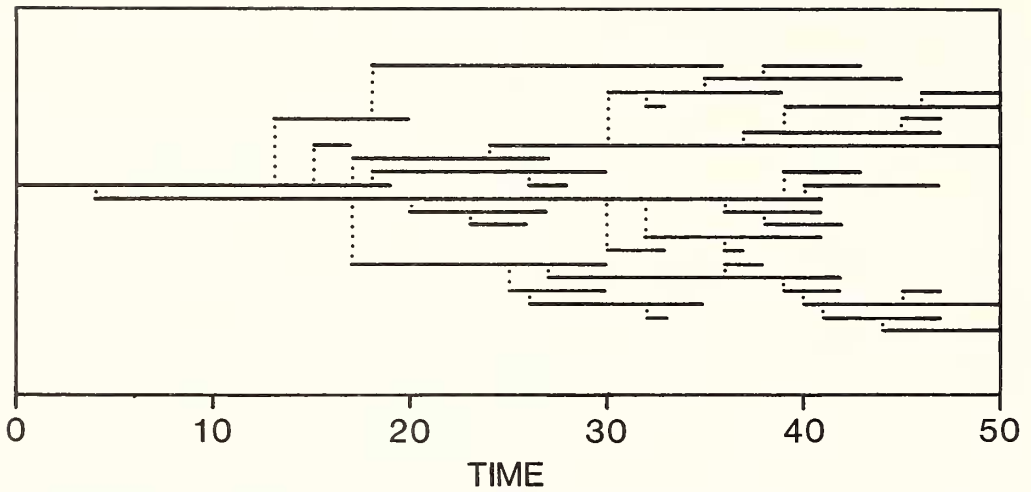
A similar model has also been developed for plant diversification (Knoll *et al.* 1979, 1984; Niklas *et al.* 1980, 1983). Kitchell and Carr (1985), in turn, proposed a nonequilibrium model of diversification. Their model is also based on the assumption of converse diversity dependence of the rates of origination and extinction within each evolutionary fauna, but the system is continually kept away from equilibrium by evolutionary innovations and mass extinctions. This model also fits the empirical pattern.

The assumption of diversity dependence, however, was questioned by Hoffman (1981, 1985*a, b*), Cracraft (1982, 1985), and Walker and Valentine (1984), on both theoretical and empirical grounds, and Hoffman (in press *a, b*) suggested a double random walk model of diversification. This model assumes that the average probabilities of speciation and species extinction per time interval behave as two random walks, i.e. vary at random and independently from each other; the average probability of speciation over the entire Phanerozoic, however, exceeds the average probability of species extinction. Given all the biases of the fossil record (Raup 1972; Signor 1982), this double random walk model cannot be rejected as a null hypothesis when tested against the empirical pattern of global diversity of marine animal families (Hoffman in press *a*).

In this paper, we wish to address the question of whether this double random walk model can account for both the shape of the curve of global diversity and the pattern of three evolutionary faunas.

SIMULATION

The essential features of the empirical pattern of marine animal diversity in the Phanerozoic are: a relatively low diversity in the Cambrian, a rapid increase in the Late Cambrian-Ordovician and fluctuating diversity through the remainder of the Palaeozoic, a drop in diversity in the Late Permian-Triassic, and an increasing diversity through the Mesozoic and Cainozoic (Sepkoski *et al.* 1981).

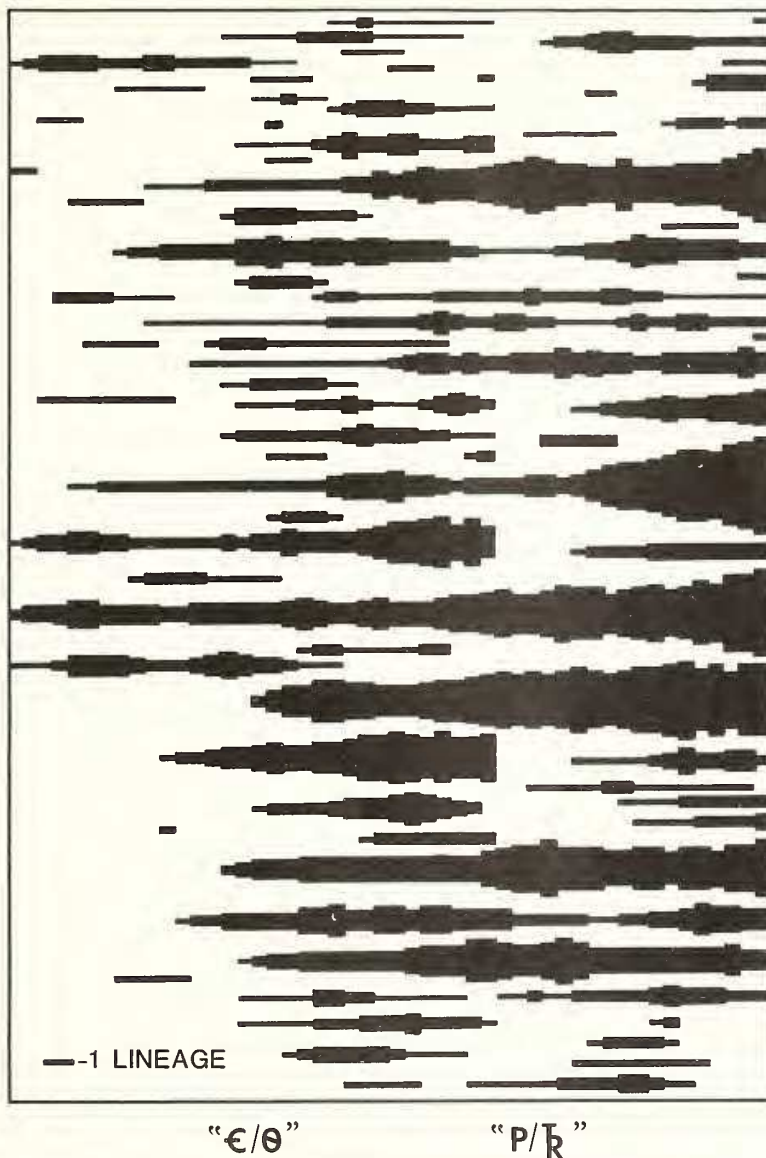


TEXT-FIG. 1. An example of random clade generation by Raup and Schopf (1978), as employed in our simulation. The number of lineages at each point in time gives the measure of clade diversity. Time is expressed in computer steps.

Given the biases of the fossil record, it is doubtful if a more detailed description of this pattern would be robust. The pattern is a net result of changes in diversity of the three evolutionary faunas (Sepkoski 1981, 1984). The Cambrian fauna achieved maximum diversity in the Middle and Late Cambrian and then gradually declined. The Palaeozoic fauna appeared in the Cambrian, rapidly proliferated in the Early and Middle Ordovician, fluctuated without any clear trend through the remainder of the Palaeozoic, suffered heavily from the Late Permo-Triassic extinction, and again fluctuated but at a much lower level in the Mesozoic and Cainozoic. The Modern fauna also appeared in the Cambrian but it continually increased in diversity throughout the Phanerozoic. It is this total pattern that needs to be reproduced by any model of diversification.

We considered seventy-five random clades (like the one illustrated in text-fig. 1). Fifty clades were taken from Raup and Schopf (1978), who generated them under the assumption that at each of the fifty time steps each lineage has a 0.1 probability of branching, a 0.1 probability of being terminated, and a 0.8 probability of persisting without any change. With use of a table of random numbers, twenty-five additional clades were produced by random coupling of these clades into pairs. Sixty of these seventy-five clades were then distributed at random along the fifty-step time axis. Thus, some long and thick clades could be reduced to minute clades if they happened to be located very close to the end of the time axis. This procedure eliminated any possible intercorrelation between the clades produced by random coupling and the original clades. The continual addition of new clades ensured that, although the probabilities of lineage origination and termination in each clade were equal and constant, the average probability of lineage origination in the entire system was greater than the average probability of lineage termination.

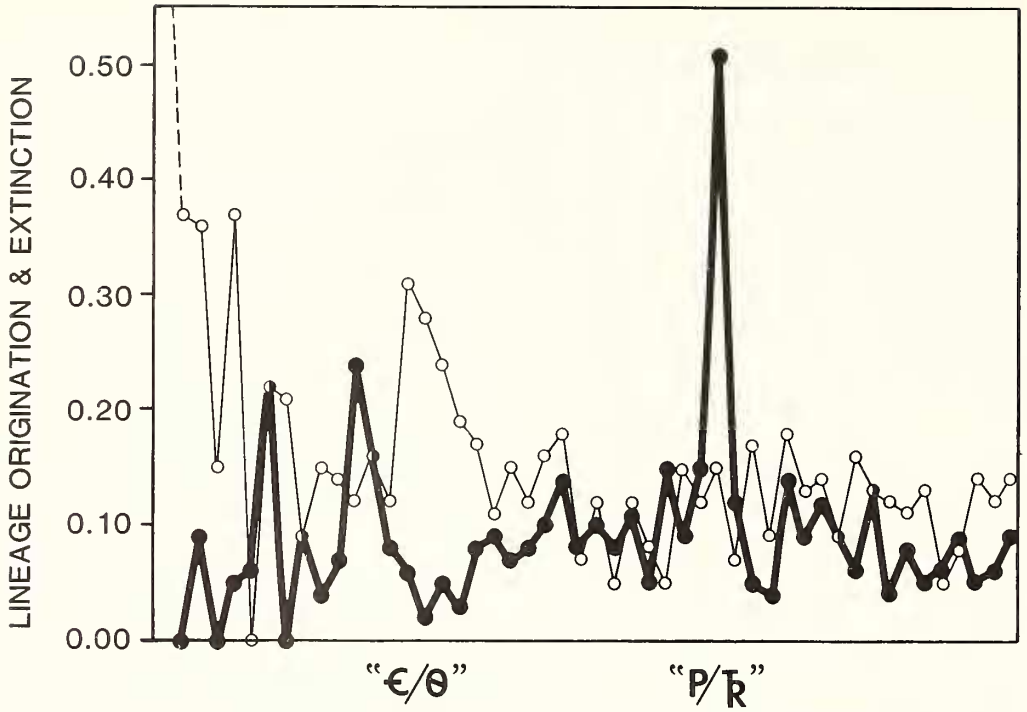
This system represents an example of the double random walk model. Biologically it implies that the average probabilities of speciation and species extinction are each determined by a myriad of biotic and abiotic factors and, therefore, change at random from one time step to another. Not surprisingly, the lineage number (standing diversity) in the system increases without showing the characteristic features of the empirical pattern of marine animal diversity. The picture changes substantially, however, when this model is supplemented with two extraordinary events representing a kind of intervention function. Fifteen randomly chosen clades were added to the system at time



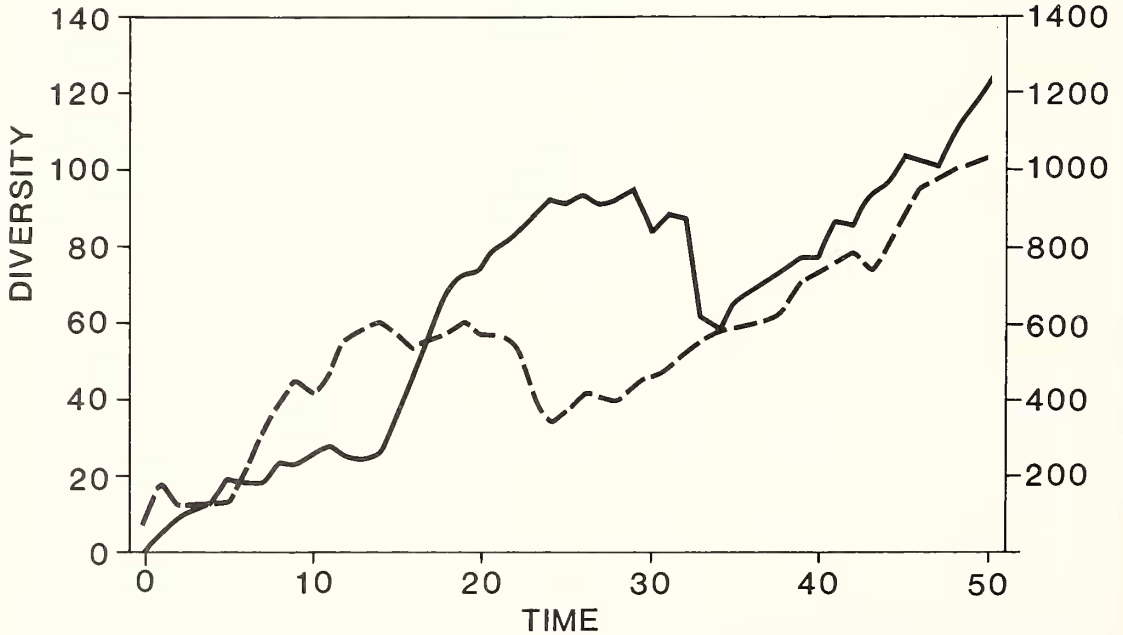
TEXT-FIG. 2. A simulated system of randomly distributed random clades affected by the 'Late Cambro-Ordovician radiation' and 'Late Permo-Triassic extinction' (see text for explanation). Time is expressed in fifty artificial steps.

steps 14, 15, and 16—to model the Late Cambro-Ordovician radiation; ten randomly chosen clades were terminated at time step 33—to model the Late Permo-Triassic extinction. One such simulation is presented in text-fig. 2.

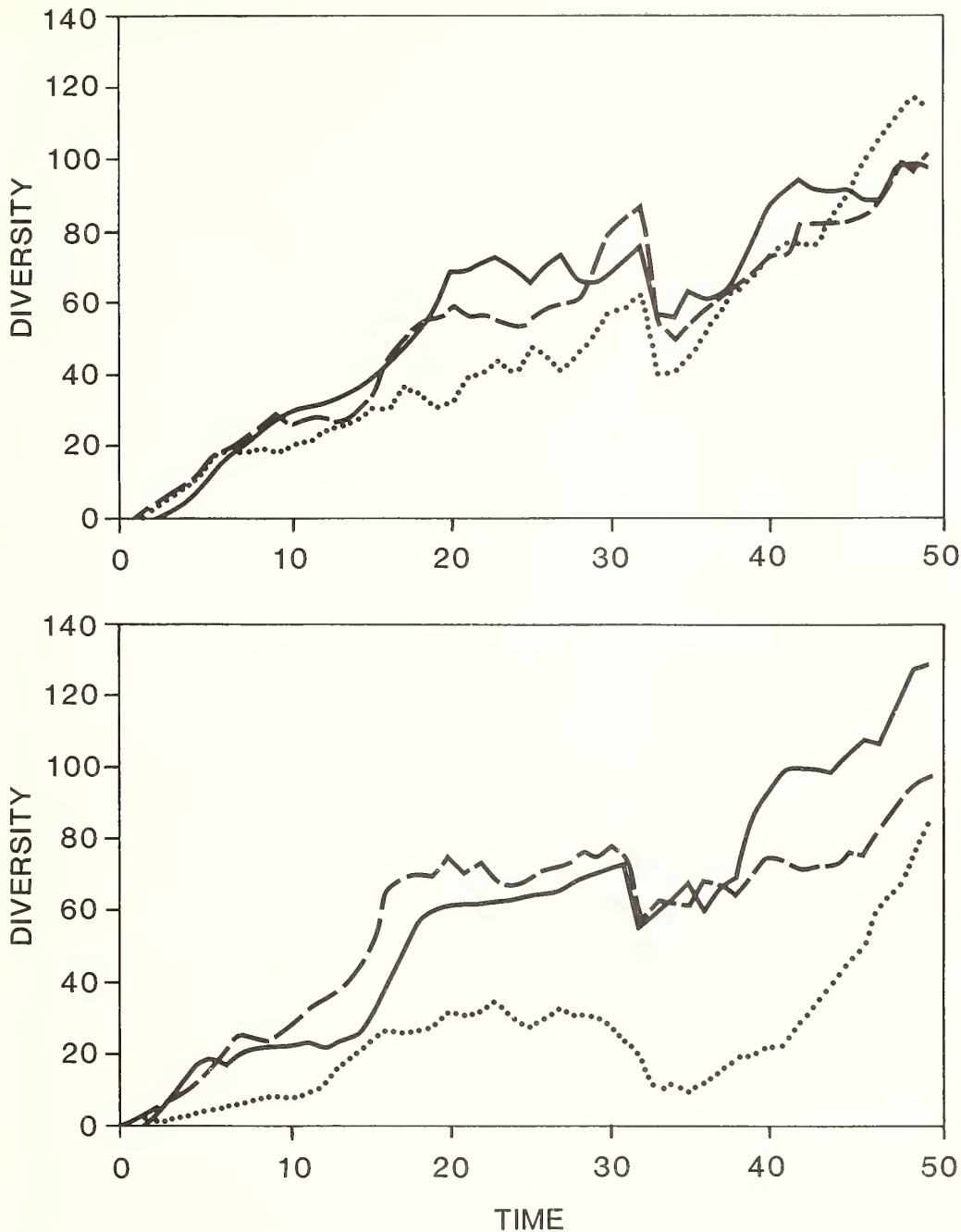
This quasi-random system corresponds to the double random walk model perturbed by two events representative of a different class of random phenomena. This is illustrated by the plot of per lineage rates of origination and extinction per time step (text-fig. 3), which shows two random



TEXT-FIG. 3. Per lineage origination (open circles) and extinction (closed circles) of lineages per time step in the system illustrated in text-fig. 2.



TEXT-FIG. 4. Total diversity (left-hand scale) of the system illustrated in text-fig. 2 (solid line) compared to the empirical pattern (dashed line) of marine animal family diversity (right-hand scale). Time is expressed in fifty artificial steps.



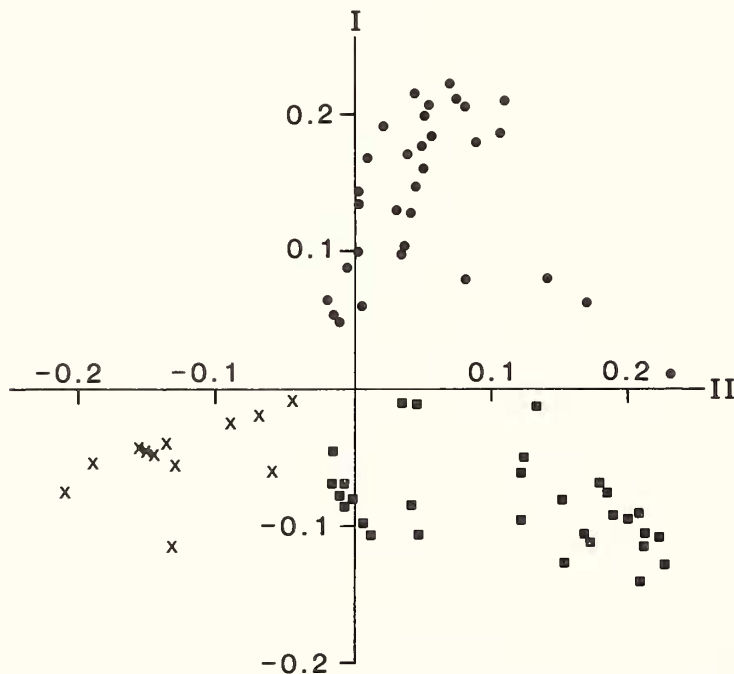
TEXT-FIG. 5. Total diversity of the system in six other simulations, additional to that illustrated in text-fig. 4.

walks, each of them with an outlier. The outliers represent historical events extrinsic to the system—mass extinctions in the analyses of Sepkoski (1984) and Kitchell and Carr (1985).

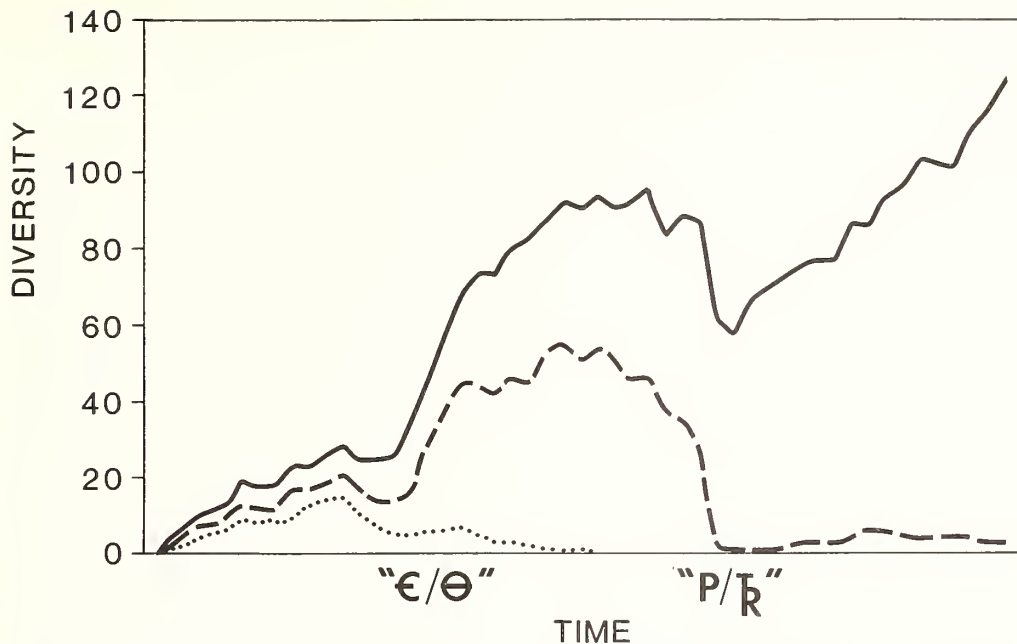
Total diversity of this system is shown in text-fig. 4. It is compared to the actual empirical pattern of marine animal diversity which, for the sake of comparability, is plotted here to the same scale and against an artificial time scale of fifty steps, rather than against absolute time in millions of years. Apart from the timing and magnitude of the 'Late Cambro-Ordovician radiation' and 'Late Permo-Triassic extinction'—which we determined arbitrarily, without much effort to tune them to the actual events—the empirical pattern does not appear to be clearly different from the simulated one. If these events were shifted five to seven steps back in time, as is needed to fit the actual events more precisely, the two patterns would match even better. Our other simulations produce, in fact, fairly similar patterns of total diversity (text-fig. 5).

The difference between the shape of the empirical curve shown by the dashed line in text-fig. 4 and the pattern shown, for instance, by Sepkoski (1984, fig. 1) reflects the effect of time scale. Our simulation assumes constant time steps. Sepkoski's empirical pattern is here plotted against the same time scale. We thus regard the absolute duration of the actual geological time intervals employed for compilation of the empirical data as one of the factors which contribute to the randomness of the entire system. Alternatively, the results of our simulation could be plotted against an absolute time scale; the pattern generated by the simulation would then also conform to the empirical pattern.

We conducted factor analyses of the system illustrated in text-fig. 2. In Q-mode analysis, which had also been used by Flessa and Imbrie (1973) and Sepkoski (1981), the first three factors accounted for 61.2%, 16.0%, and 7.8% of the total variance respectively (85% jointly). In R-mode analysis, the first three factors accounted for 32%, 16.2%, and 11.2% of the total variance respectively (about 59% jointly). All clades were classified into three groups according to their loadings in R-mode



TEXT-FIG. 6. Scattergram of clade loadings on the first two factors of the system illustrated in text-fig. 2. Differential graphic symbols denote three groups of clades which are comparable to 'evolutionary faunas'.



TEXT-FIG. 7. Total diversities of three groups of clades identified by factor analysis of the system illustrated in text-fig. 2.

analysis (text-fig. 6), and the total diversities of these three groups of clades were plotted against time (text-fig. 7).

Clearly, the smallest group includes the clades which attained their maximum diversity very early in the history of the system, generally prior to the 'Late Cambro-Ordovician radiation'. The second group comprises the clades which expanded prior to, and suffered from, the 'Late Permo-Triassic extinction'. The largest group includes the clades which were not affected by the 'Late Permo-Triassic extinction' and expanded chiefly after that event. This pattern strongly resembles the pattern of three evolutionary faunas identified by factor analysis of the actual data on marine animal diversity. Our groups of clades, however, do not show any diversity dependence and do not interact with each other.

R-mode factor analysis of our other simulations resulted in the first three factors accounting for 40–60% of the total variance (Q-mode analysis generally accounted for 20–30% more), and the grouping of clades was also primarily determined by the relationship of individual clades to the 'radiation' and 'mass extinction' events.

DISCUSSION

These results suggest that the essential features of the empirical pattern of marine animal diversification in the Phanerozoic can be mimicked by a double random walk model perturbed by one 'radiation' and one 'mass extinction' event. The difference between our simulation and Sepkoski's (1981) factor analysis of the actual data is remarkably small. In Q-mode analysis, the first three factors extracted from our quasi-random data account for approximately 85% of the total variance. The first three factors of the actual data on Phanerozoic diversification account for about 91% of the total variance. This small disparity may not suggest any major difference in the degree of nonrandomness between our simulation and family diversity patterns in the Phanerozoic.

In our simulation, we may encounter a scaling problem because our randomly generated clades are often considerably smaller than the actual classes analysed by Sepkoski (1981). A similar problem was pointed out by Stanley *et al.* (1981) who discussed the effect of unrealistic probability distributions and clade sizes on the shape of the random clades generated by Gould *et al.* (1977) under the assumption of equilibrium diversity. This effect, however, does not appertain to our results for two reasons: first, the clades we considered had been generated by Raup and Schopf (1978) without the equilibrium constraint; and second, the structure revealed by factor analysis in our system of randomly distributed clades depends primarily upon the extrinsic perturbations rather than upon details of the shape of individual clades.

Of course, the fact that our simulation can reproduce the essential features of the empirical pattern does not demonstrate the validity of the double random walk model of diversification. It shows only that this stochastic model may provide an adequate explanation and, therefore, that analysis of these features of the pattern cannot point to the process of diversification. Much more detailed pattern analysis would be needed to this end. Given all the biases of the fossil record, however, and the uncertainty about the absolute calibration of the geological time scale, a detailed pattern analysis might give more weight to statistical noise than to real evolutionary phenomena.

The empirical pattern of marine animal diversification in the Phanerozoic, and the underlying pattern of three evolutionary faunas, may reflect a myriad of independent biological factors, environmental events, and biases of the fossil record rather than an orderly process.

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